Abstract and Keywords

Cognitive neuroscience research has begun to address the potential interaction of brain networks supporting creativity by employing new methods in brain network science. Network methods offer a significant advance compared to individual region of interest studies due to their ability to account for the complex and dynamic interactions among discrete brain regions. As this chapter demonstrates, several recent studies have reported a remarkably similar pattern of brain network connectivity across a range of creative tasks and domains. In general, such work suggests that creative thought may involve dynamic interactions, primarily between the default and control networks, providing key insights into the roles of spontaneous and controlled processes in creative cognition. The chapter summarizes this emerging body of research and proposes a framework designed to account for the joint influence of controlled and spontaneous thought processes in creativity.

Keywords: creativity, cognitive neuroscience, default network, control network, brain connectivity, cognition

Creativity is a seemingly complex and mysterious construct, and the neuroscience of creativity has proven similarly elusive in its quest to capture creativity in the brain. Seminal meta-analyses reported activations of brain regions spanning most of the cortex, raising questions about whether creativity can be reliably distilled to a discrete area of the brain (Arden, Chavez, Grazioplene, & Jung, 2010; Dietrich & Kanso, 2010). These inconclusive findings also fueled enduring questions surrounding the role of cognitive control in creative thought, as several studies reported activation of brain regions linked to both cognitive control and spontaneous thought. Many studies implicated regions of the brain’s default network, a set of brain regions associated with spontaneous and self-generated cognition (Beaty et al., 2014; Ellamil, Dobson, Beeman, & Christof, 2012; Jung, Mead, Carrasco, & Flores, 2013; Takeuchi et al., 2011, 2012; Wei et al., 2014). On the other hand, a similarly large literature implicated regions of the executive control network, a set of regions linked to focused attention and cognitive control (Benedek et al., 2014a; Ellamil et
Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

al., 2012; Fink et al., 2012; Jung et al., 2013; Takeuchi et al., 2010). Notably, a majority of past research assessed the isolated contribution of individual brain regions, so whether these regions interacted to support creative thought remained unclear.

Networks of the Brain and Relevance to Creative Cognition

The human brain is comprised of several interacting large-scale networks (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016). Networks consist of brain regions that are spatially distributed but correlated with one another through structural or functional interactions. Such networks are often studied using resting-state functional magnetic resonance imaging (fMRI), a technique that involves acquiring spontaneous fluctuations in blood-oxygen-level-dependent (BOLD) signals as participants relax, awake in the scanner, without performing a cognitively engaging task. Critically, networks identified at rest have been shown to contribute to basic cognitive and perceptual processes in task-based fMRI, suggesting an interaction between default and executive control networks across human cognition (Cocchi, Zalesky, Fornito, & Mattingley, 2013). Here, we focus primarily on functional networks with potential relevance to creative cognition and artistic performance, namely the default and executive control networks.

The first network to be described in the neuroimaging literature was the so-called default mode network or default network (Raichle et al., 2001; Shulman et al., 1997). The default network consists of midline and posterior inferior parietal brain regions, and its activity is associated with self-referential or “self-generated” thought, including mind-wandering, daydreaming, episodic memory retrieval, episodic future thinking, and mentalizing, among others (Andrews-Hanna, Spreng, & Smallwood, 2014; Buckner, Andrews-Hanna, & Schacter, 2008; Stawarczyk & D’Argembeau, 2015). The default network is thus characterized by internally focused mental activity that occurs in the absence of external stimulation (i.e., stimulus-independent thought; Giambra, 1995). Several neuroimaging studies have reported activation of default regions during both creative cognition and artistic performance (for reviews, see Beaty, Benedek, Silvia, & Schacter, 2016a; Gonen-Yaacovi et al., 2013; Wu et al., 2016). In light of the default network’s role in imaginative thought (e.g., daydreaming), researchers hypothesize that its activation during creative thinking tasks reflects spontaneous or self-generated thought (Abraham, 2014; Beaty et al., 2014; Benedek et al., 2014a; Chen et al., 2014; Chen et al., 2015; Ellamil et al., 2012; Jauk, Neubauer, Dunst, Fink, & Benedek, 2015; Jung et al., 2013; McMillan, Kaufman, & Singer, 2013; Mok, 2014).

The executive control network is another core network of the brain. Comprised of lateral prefrontal and anterior inferior parietal regions, the control network shows activation during experimental tasks that require externally-focused attention and cognitive control, such as working memory, response inhibition, task-set switching, and goal maintenance (Seeley et al., 2007). Regions of the control network have been implicated in structural and functional neuroimaging studies of creativity (Wu et al., 2016), consistent with behav-
Brain Networks and Creative Cognition

Brain network research has provided key insights into the neural basis of higher-order cognition, including core human attributes such as intelligence and personality (Beaty et al., 2016b; van den Heuvel, Stam, Kahn, & Pol., 2009). A network approach can reveal the extent to which the interaction of distributed brain regions gives rise to various cognitive processes. Several recent studies have embraced network methods to examine network interactions underlying domain-general creative cognition (e.g., divergent thinking). As noted earlier, seminal research on the structural and functional correlates of creative
Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

thought yielded a rich but largely inconsistent body of work (Arden et al., 2010; Dietrich & Kanso, 2010). Such work implicated a diffuse set of brain regions associated with a range of cognitive processes. Critically, researchers often reported the involvement of both default and control network regions, raising questions about whether creative thought was more a product of spontaneous thought or cognitive control (Jung et al., 2013). Moreover, the extent to which creative cognition involved cooperation among default and control network regions remained unclear, as these networks have shown both cooperation and competition during resting-state and task-based fMRI (Cocchi et al., 2013).

To address this question, a recent study explored brain network dynamics underlying performance on a divergent thinking task (Beaty, Benedek, Kaufman, & Silvia, 2015). Using a task paradigm similar to past research (e.g., Fink et al., 2009), the authors asked participants to think of alternate uses for common objects (i.e., divergent thinking) or to simply think about the physical properties of objects; the resulting task contrast revealed brain regions engaged during the creative transformation of objects while controlling for activity related to simple semantic processing and/or mental imagery. Whole-brain functional connectivity analysis was used to contrast differences in voxel-to-voxel connectivity between the two tasks. Notably, this approach could not provide information about which specific brain regions were correlated during performance of the task, nor could it reveal potential temporal differences in connectivity between regions across the task duration. Thus, a series of post hoc analyses were conducted using regions of interest (ROIs) identified in the whole-brain analysis.

The whole-brain results revealed a network of regions that showed connectivity differences during divergent thinking compared to the control task. This network included several core hubs of the default (precuneus and posterior cingulate cortex [PCC]) and control (right dorsolateral prefrontal cortex [dLPC]) networks, among other regions (see Figure 21.1A). To confirm the network affiliation of these voxel clusters, the authors conducted resting-state functional connectivity analysis, using the peak coordinates of the ROIs from the whole-brain analysis; this analysis used resting-state fMRI data from an independent sample of age-matched participants. The results confirmed the hypothesized resting-state network affiliation of the three ROIs: both the precuneus and PCC showed positive coupling with other regions of the default network (medial prefrontal cortex [mPFC] and bilateral inferior parietal lobe [IPL]) and salience network (anterior cingulate cortex [ACC] and bilateral insula); in contrast, these regions showed negative coupling with the control network (i.e., dLPC and bilateral anterior IPL). Likewise, the right dLPC showed positive coupling with other regions of the control network and negative coupling with default regions.

Having confirmed the network affiliation of the ROIs, the authors then examined their connectivity with other regions during the divergent thinking task, using both static and dynamic network analysis. Regarding static connectivity, the results showed increased functional connectivity between the default ROIs and regions of the control and salience networks (see Figure 21.1B). Similarly, the right dLPC showed increased connectivity
with regions of the default network. To determine whether these patterns of connectivity were constant (static) or dynamic, the authors employed a temporal connectivity analysis that divided the task into several two-second time bins, corresponding to the fMRI acquisition time (i.e., TR). Results revealed a dynamic pattern of coupling that unfolded across the task duration (see Figure 21.1C). Both the PCC and precuneus showed early coupling with salience network regions (i.e., bilateral insula) and later coupling with control network regions (i.e., dIPFC), pointing to delayed interaction between default and control regions. This temporal pattern was mirrored in the dIPFC, which only showed connectivity differences later in the task, including coupling with default regions (PCC and left IPL). Taken together, the results point to a cooperative and dynamic contribution of the default and control networks to divergent thinking.

The notion that creative cognition involves interactions of the default and control networks received further support from two recent studies (Green, Cohen, Raab, Yedibalian, & Gray, 2015; Mayseless, Eran, & Shamay-Tsoory, 2015). Green and colleagues adopted the classic verb generation task, which involves generating verbs (i.e., actions) in response to a series of presented nouns (i.e., things). The task was modified to assess creative cognition by asking participants to “think creatively” when generating verbs, or to simply generate a typical verb in response to nouns; latent semantic analysis was then used to quantify the semantic distance between the nouns and verbs in each condition. Results showed that compared to generating typical verbs, generating creative verbs was associated with greater activation in several brain regions, including the mPFC, a core hub of the default network. Critically, a functional connectivity analysis revealed that, as the semantic distance between the nouns and verbs increased in the creative condition, the mPFC showed stronger coupling with the dorsal anterior cingulate cortex (dACC)—a brain structure commonly associated with executive control. These findings suggest that the ability to flexibly combine conceptual information involves increased cooperation of brain regions linked to spontaneous thought and cognitive control.
Figure 21.1. Default network interactions during divergent thinking. (A) A whole-brain network associated with divergent thinking, including several default regions (e.g., posterior cingulate). (B) The posterior cingulate shows increased coupling with control (e.g., dorsolateral prefrontal cortex) and salience (e.g., insula) network regions across the task duration. (C) Temporal analysis reveals early coupling of the posterior cingulate with salience regions and later coupling with control regions, among others. ACC = anterior cingulate cortex; ANG = angular gyrus; DLPFC = dorsolateral prefrontal cortex; IPL = inferior parietal lobe; MTG = middle temporal gyrus; PMC = pre-motor cortex; RLPFC = rostrolateral prefrontal cortex; STG = superior temporal gyrus. (See Color Insert)
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Additional support for this proposal comes from another recent fMRI study of divergent thinking (Mayseless et al., 2015). This study sought to assess brain activity and functional connectivity associated with the originality of divergent thinking responses—defined as the relative rarity of the response. Similar to other task paradigms (Beaty et al., 2015; Fink et al., 2009), participants were presented with common objects and were asked to either generate alternate uses (i.e., divergent thinking) or to generate physical characteristics of the objects. Participant responses were coded for originality by trained raters, permitting an analysis of brain activity and connectivity related to the ability to generate uncommon ideas. Results showed that originality scores were associated with increased activation of default network regions, including the mPFC and the PCC. Moreover, a functional connectivity analysis showed that originality was related to greater coupling of the dACC with the occipital-temporal region. Taken together with the results of Beaty et al. (2015) and Green et al. (2015), these findings provide support for the cooperative role of brain regions involved in cognitive control and spontaneous thought during creative cognition. Moreover, it highlights a possible progression of functional connectivity from networks linking novelty generation (i.e., default network) with focused attention (i.e., salience network), and progressing to networks associated with the implementation of ideas (i.e., control network).
Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

This neuronal progression from novelty generation to implementation/execution is at the core of the major advance provided by network perspectives within the creativity neurosciences. Additionally, the integration of various brain networks in the execution of creative ideas likely explains the lack of specificity apparent in previous reviews focused on static measures of discrete brain-behavior correlates of creative cognition. These reviews, which covered structural, functional, and lesion studies, all showed widespread patterns that lacked sufficient specificity—whether by virtue of hemisphere, lobe, or region—regarding how creative cognition is organized in the human brain (Arden et al., 2010; Dietrich & Kanso, 2010). Just as creativity has been hypothesized to involve discrete stages of preparation, incubation, illumination, and evaluation (Poincare, 1913), its manifestation in the human brain involves the dynamic interaction of networks that plausibly underlie these broad cognitive constructs.

Brain Networks and Artistic Performance

A growing body of research has explored the brain basis of artistic performance. But like the literature on domain-general creativity, this literature was initially marked by seemingly contradictory findings. Neuroimaging studies of musical improvisation, for example, reported activation of regions within the default and control networks (see Figure 21.2), raising questions about whether improvisation involved more or less cognitive control (Beaty, 2015). In a striking illustration of this paradox, Limb and Braun (2008) and Berkowitz and Ansari (2008) published results within the same year with widely diverging conclusions. While Limb and Braun (2008) reported widespread deactivation of control network regions and increased activation of default regions, Berkowitz and Ansari (2008) reported increased activation of several regions involved in cognitive control. Such conflicting findings raised questions about whether musical improvisation required cognitive control, spontaneous thought, both, or neither.

Figure 21.2. Visualization of brain activation peaks reported in fMRI studies of improvisation. Highlighted regions indicate areas with activation reported in at least two of the seven studies included in the figure. Note that several activations are located within regions of the default network (anterior prefrontal cortex) and control network (dorsolateral prefrontal cortex). (See Color Insert)
To address this paradox, a recent study assessed brain network interactions during musical improvisation (Pinho, Ullén, Castelo-Branco, Fransson, & de Manzano, 2016). Professional pianists improvised on an MRI-compatible keyboard during two experimental conditions. One condition presented a specific set of piano keys (or “pitch sets”); participants used only these keys to generate melodic sequences. The other condition presented emotional cue words (e.g., “joy”); participants were asked to express the given emotion during improvisation. The authors used functional connectivity analysis with the dlPFC as a region of interest to assess its interaction with other brain regions during each condition. Compared to the emotion condition, the “pitch set” condition revealed increased connectivity between the dlPFC and regions associated with motor planning control (e.g., pre-supplementary motor area). Conversely, the emotion condition was associated with increased coupling between the dlPFC and regions of the default network (e.g., mPFC and PCC). These findings suggest that improvisation involves cooperation between control and default network regions during the strategic expression of emotion.

Further evidence for the cooperative role of the default and control networks comes from a recent study of poetry composition (Liu et al., 2015). Here, professional poets were asked to spontaneously generate new lines of poetry in one condition, and then to revise their previously generated poetry in another condition. To explore brain networks associated with both conditions, the authors used independent component analysis (ICA)—a data-driven method used to identify spatially and temporally distinct clusters of brain regions (i.e., networks). ICA revealed brain networks associated with overall task performance; one included default network regions, and another included control network regions. During idea generation, the default and control network clusters were negatively correlated. During idea revision, however, the correlation between the networks increased significantly. Thus, the results demonstrate task-specific differences in network dynamics underlying two key aspects of poetry composition, with default-control network coupling associated with the strategic revision of spontaneously generated ideas.
Brain network dynamics also have been explored during artistic drawing (Ellamil, Dobson, Beeman, & Christoff, 2012). This study employed a similar paradigm as the poetry composition study to examine network interactions involved in the generation and evaluation of visual art. Using an MRI-compatible drawing pad, semi-professional visual artists generated (sketched) ideas for a book cover based on a series of descriptions, and then evaluated these sketches in a separate condition. Results revealed that idea generation recruited several regions of the default network, whereas idea evaluation simultaneously recruited regions of both the default and control networks. Critically, a functional connectivity analysis revealed increased coupling between default and control regions during idea evaluation. These findings are consistent with the poetry composition study of Liu et al. (2015), and suggest that the default and control networks show increased cooperation when artists engage in the critical evaluation of self-generated ideas. Such work is also consistent with the interaction of default and cognitive control networks during creative cognition, with generative aspects being associated with decoupling, and implementation (e.g., planning and goal maintenance) components being associated with increased coupling between default and control networks (Beaty et al., 2015).

Cognitive Control, Spontaneous Thought, and the Creative Brain

In this chapter, we explored the contribution of large-scale brain networks in creative cognition and artistic performance. Across both domain-general and domain-specific contexts, we provide consistent evidence that creative thought is a product of dynamic interactions between the default and control networks. In general, we contend that the default network influences creative idea generation via spontaneous and self-generated thought, while the control network constrains and directs this process via top-down monitoring and executive control. This proposal is consistent with a growing number of studies showing default-control network coupling during goal-directed, self-generated thought. Taken together, this research helps to resolve long-standing questions in the creativity literature regarding the contributions of cognitive control and spontaneous thought in creative cognition. It also provides a path forward toward research designed to better understand the generative and evaluative components underlying creative expression.

We described evidence from several recent fMRI studies reporting default-control network coupling during domain-general creative cognition (Beaty et al., 2015; Green et al., 2015; Mayseless et al., 2015). For example, Beaty and colleagues showed increased functional connectivity between regions of the default and control networks during divergent thinking, and a temporal connectivity analysis revealed dynamic coupling of these regions at different stages of the task. In this context, default network activity may reflect the spontaneous retrieval of information from episodic and semantic memory, and its coupling with the control network may in turn reflect executive mechanisms recruited to monitor, direct, and integrate such information into coherent and goal-congruent responses. Without sufficient top-down control, idea production may rely solely on sponta-
Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

neous thought, which could result in the retrieval of salient but unoriginal concepts from memory (or alternatively, highly original but not relevant concepts).

Behavioral research has shown that common (and thus unoriginal) ideas tend to occur at early stages of divergent thinking, as people recall known uses for objects from memory (Gilhooly et al., 2007). However, this effect is markedly attenuated in people with greater executive resources (Beaty & Silvia, 2012), suggesting that cognitive control is required to inhibit salient conceptual information and manage complex search processes. At the other extreme, psychopathology (e.g., schizophrenia) can be characterized by highly original but irrelevant ideas (e.g., neologisms), resulting from insufficient top-down control narrowing information flow to meet task demands. Although this evidence comes from behavioral research, it may help to account for neuroimaging findings that reported executive network coupling with default regions during divergent thinking. Similarly, dysregulation between default and cognitive control networks may help to explain the tantalizing (but controversial) overlap between creative cognition and psychopathology (Abraham, 2015; Jung, Grazioplene, Caprihan, Chavez, & Haier, 2010; Jung, 2014).

Default-control network cooperation has also been reported during artistic performance, but such coupling appears to depend on task goals and constraints. On the one hand, Liu et al. (2015) reported a negative association between these networks during the spontaneous generation of poetry. On the other hand, Ellamil et al. (2012) found increased connectivity between default and control regions when visual artists evaluated their ideas, and Pinho et al. (2016) found a similar pattern when pianists were asked to tailor their improvisations based on specific emotional cues. In both studies, artists were given an explicit task goal that required them to constrain their thought process, presumably leading to increased top-down processing stemming from the control network. Conversely, Liu et al. (2015) simply asked poets to spontaneously generate poetry and did not impose specific goals, which might have relaxed top-down constraints, possibly reflected in deactivation of the control network. Thus, the control network’s coupling with the default network appears to depend on the extent of goal-directed processing required for a given creative task.

Conclusion and Future Directions

Although the default and control networks have shown consistent involvement in neuroimaging studies of creative cognition, the specific cognitive functions underlying their activity remain unclear. This lack of clarity presents an opportunity for neuroimaging researchers to add significant understanding to this nascent field. Because the default network is associated with various self-generated thought processes, an important direction for future research is to determine which of these processes are relevant to creative cognition. Recent behavioral research points to a role for episodic memory in divergent thinking (Addis, Pan, Musicaro, & Schacter, 2016; Madore, Addis, & Schacter, 2015), suggesting that people may draw upon and flexibly combine episodic content to construct novel mental representations (Madore, Gaesser, & Schacter, 2014; Madore & Schacter,
Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

2016; Schacter & Madore, 2016). In addition, investigation of the mechanisms underlying control network activity in creativity presents a vast number of opportunities regarding such issues as timing, sequencing, and intensity at various stages of the creative process. Are the interactions between default and cognitive control networks similar for creative pursuits in the arts and sciences? Are they the same across males and females, as well as younger versus older individuals? Can these interactions be modified through external behavioral, pharmacological, or electrical stimulation? Ultimately, we believe a critical direction for future research is to further characterize the brain network dynamics that give rise to creative cognition and artistic performance. In our view, this line of research shows the greatest promise in understanding the roles of cognitive control and spontaneous thought within the creative brain.

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References


Interacting Brain Networks Underlying Creative Cognition and Artistic Performance


Interacting Brain Networks Underlying Creative Cognition and Artistic Performance


Interacting Brain Networks Underlying Creative Cognition and Artistic Performance


Interacting Brain Networks Underlying Creative Cognition and Artistic Performance


Interacting Brain Networks Underlying Creative Cognition and Artistic Performance

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